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Introductions and their place in British wildlife

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The topic of introductions and invasions is a wide one, and has been the subject of much debate among ecologists in recent years, with a Royal Society discussion meeting on biological invasions in 1986 (Kornberg & Williamson 1987), a British Ecological Society meeting on colonisation, succession and stability (Gray, Crawley & Edwards 1987), which also paid close attention to the impact of invaders, and a Mammal Society/Fauna and Flora Preservation Society symposium on reintroductions of mammals in 1986 (Anon 1986).

Some of the most dramatic recent incidents of long-range introductions are in Africa, and, while not having space to examine them in detail, they serve as a reminder that we have in no sense 'learnt our lesson' from ecological disasters at home and abroad. Slipshod quarantine procedures, inadequate fumigation of aircraft, and careless pet and livestock keepers are as prevalent as ever. The massive increase in global travel and the speed of commerce – fresh *mange-tout* with fresh long-tailed blue butterfly (*Lampedes boeticus*) caterpillars in our supermarkets every week – mean that the opportunist plant or animal can reach Britain more easily than ever before.

Concentrating on impacts on *wildlife* neglects the problems that agriculture and forestry face from aliens. Most pests of crops in Britain are not native species, and British species have often become serious agricultural pests when introduced elsewhere in the world (eg molluscs in Australia (Baker 1989), New Zealand (Barker 1989) and USA (Barrett, Byers & Bierlein 1989)); this is a signpost to an underlying pattern to be discussed later.

Excluding the above topics, what remain are the diverse impacts of introduced species as environmental factors on the native British flora and fauna.

Crucial to the discussion of introductions is Britain's island status. Many of the species that we regard as introductions reached the adjacent Continent by their own efforts several thousand years ago. It was only the English Channel and the North Sea, a peculiarity of the present inter-glacial, that necessitated human assistance for their transport to Britain.

To quantify the effect of being an island, the native fauna and flora of Britain and of Ireland can be compared with that of an equal area of the adjacent

Table 1. Numbers of species in selected animal groups native in Ireland, Britain, an equivalent Continental area (defined in Figure 1) and western Europe (where figures are available). Data from distribution maps in the following publications: Corbet and Ovenden (1980), Stebbings (1988), Peterson, Mountford and Hollom (1983), Arnold and Burton (1978), Maitland (1977), Kerney and Cameron (1979), Higgins and Riley (1983)

Group	Ireland	Britain	Continental equivalent area	W Europe
Quadruped mammals	11	26	42	103
Bats	6	14	22	30
Breeding birds	126	186	221	347
Reptiles	1	6	15	49
Amphibians	3	6	16	39
Freshwater fish	20	31	42	153
Land molluscs	66	95	147	*
Butterflies	29	62	126	349

* Data not available

Table 2. Numbers of species in selected vascular plant groups native in Ireland, Britain, an equivalent continental area (defined in Figure 1) and western Europe. Data from *Atlas Florae Europaeae* (Jalas & Suominen 1972–86)

Group	Ireland	Britain	Continental equivalent area	W Europe
Pteridophyta	55	66	70	142
Gymnospermae	2	5	4	38
Ranunculaceae	27	38	55	291
Caryophyllaceae (Sandworts, etc)	28	53	60	308
Caryophyllaceae (Campions, etc)	7	19	31	404
Other Centrospermae	18	27	37	103
Amentiferae (Salix, etc)	23	35	38	125
Polygonaceae	20	28	30	77

Continental mainland. Figure 1 shows such an area, of approximately the same areal extent as Britain and Ireland, based on the 50 km squares of the Universal Transverse Mercator Grid, and lying closest to south-east England (the most likely point of entry of terrestrial post-glacial colonists). Tables 1 and 2 illustrate the paucity of the British fauna and flora compared with the Continental mainland (both the 'equivalent area' of Figure 1, and western Europe as a whole), and the further reduction in diversity in Ireland, due at least in part to an additional post-glacial sea barrier (Godwin 1975).

Being an island has also shaped the history of Britain: 'after the discovery of America and the ocean routes to Africa and the East, Britain lay at the centre of the new maritime movement' (Trevelyan 1926). A maritime nation was more inclined to exploration and trade by sea (Morrill 1988) and, in consequence, Britain probably received its first trans-atlantic immigrants sooner than most other European countries. The range and diverse origins of garden plants today is breathtaking; but at least as amazing

is how many of them had reached Britain by the 18th century.

By contrast with the British Isles, a few island groups are noted for their endemic biotic diversity, and have suffered catastrophically from the impact of introductions. These are *oceanic* islands, such as Hawaii, New Zealand and Galapagos, where species have been isolated for long enough to have speciated, and in some cases radiated extensively. As a very recent *continental* island, Britain has few endemics, and almost all of them are the final remnant of a formerly much wider geographic range.

A feature of oceanic islands which permits a high incidence of endemism is the absence of mammalian predators and scavengers. Most island-endemic birds have evolved without the pressures of rodents, cats and mustelids, and thus are very vulnerable to their introduction. There appear to be conspicuous 'empty niches' which these and other invaders such as feral goats (*Capra hircus*) are able to fill, or niches occupied by 'inept' animals: birds or reptiles

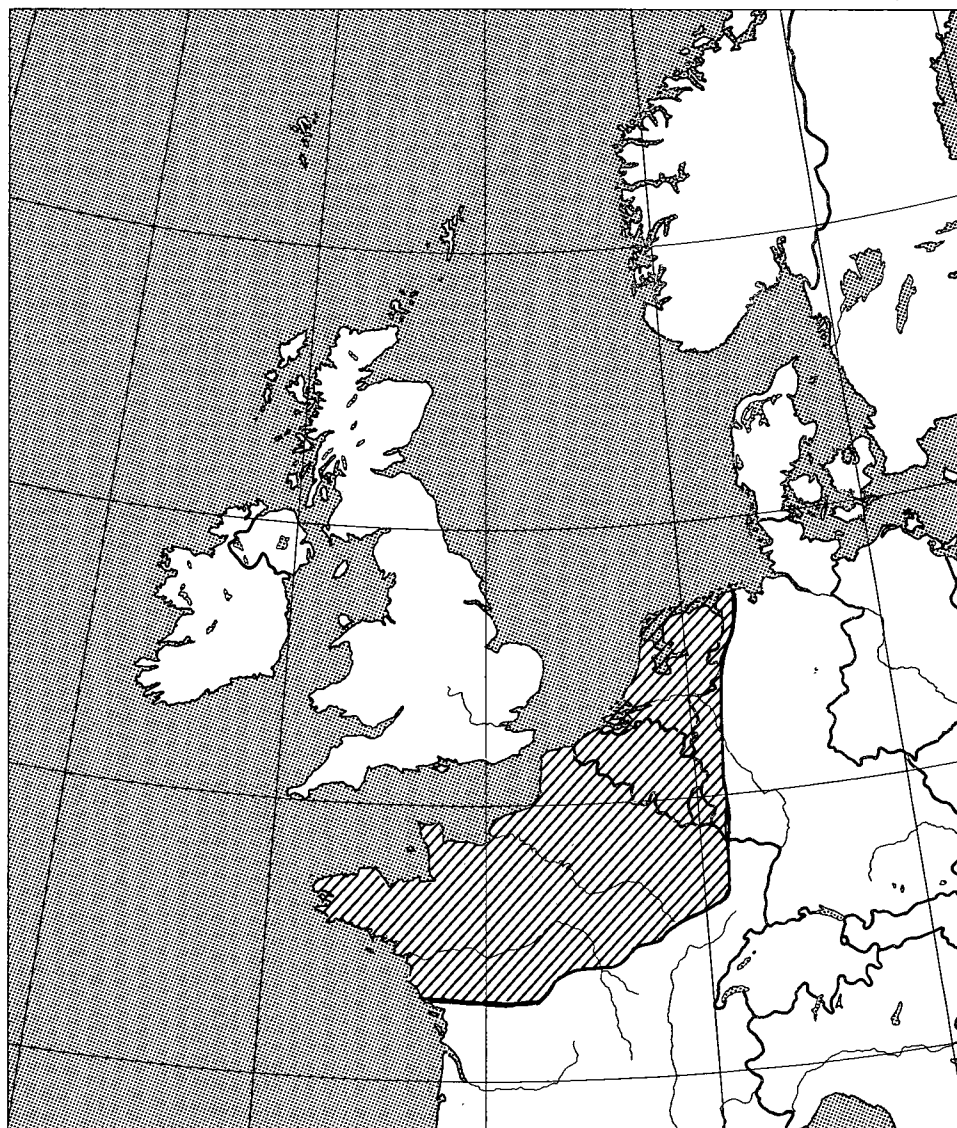


Figure 1. The British Isles and north-west Europe, with an approximately equivalent land area on the Continent adjacent to Britain shaded; this is the area used in the compilation of Tables 1 and 2

occupying niches usually associated with mammals are easily out-competed.

To put Britain's many aliens into a broader context: the native Hawaiian avifauna can be accounted for by only one successful colonist every 350 000 years (Elton 1958; Mollison 1986). Similarly, the large numbers of endemic species on islands in the Mediterranean (such as c 160 flowering plants on Crete, 10% of the native flora (Turrill 1929; Polunin 1980)) or off North Africa (blue chaffinch (*Fringilla teydea*) and endemic chat (*Saxicola dacotiae*) on the Canary Isles, 16 species of snails (Collins & Wells 1987) and 25 species of *Cylindroiulus* millipedes (Enghoff 1982) on Madeira) are all indicative of a long and stable history. The main difference in this case is latitude: the islands are far enough south to have escaped the many glaciations which repeatedly erased the temperate fauna and flora from the land which is now Britain.

WHAT IS 'NATIVE'?

Most definitions of 'native' simply mean that a species arrived unaided by man. Unfortunately, that is very hard to prove, unless the arrival itself is witnessed. Webb (1985) discussed the criteria for assuming native status for vascular plants and clarified the definition. To be native, a species must either have arrived here before the Neolithic period (c 5000 BP (before present)), when man first began farming here, or have arrived since then completely independent of man's activities. An alien is thus a species whose arrival is a consequence of the activities of man or his domestic animals.

An additional qualifier would be that species should successfully reproduce in Britain. Regular non-established migrants, such as clouded yellow butterflies (*Colias* spp.), and non-breeding residents, such as the mouse-eared bat (*Myotis myotis*) in Sussex or the black-browed albatross (*Diomedea melanophris*) in the Shetlands, are barely natives. As the individuals involved are unlikely to play any part in producing future generations, they are of minimal conservation value except as publicity, but they could help to form the nucleus of an establishing population, or function as a 'honeypot' for colonial species.

Wintering birds are a special case. For many species, Britain plays a vital role as the main feeding area, maintaining the condition of a population, outside the breeding season. Despite this importance, they will not be considered further in this paper, although it is possible for winterers to become resident, eg occasional fieldfares (*Turdus pilaris*) and bramblings (*Fringilla montifringilla*) (Sharrock 1976), or twite (*Carduelis flavirostris*) (Marshall, Lynes & Limbert 1989), in the lowlands.

A change in climate could, of course, alter the status of many of these migrant species. Last century, it seems the continental race, subspecies *gorganus*, of the swallowtail butterfly (*Papilio machaon*) was estab-

lished in Kent and adjoining counties for several successive years, but at present it is only an occasional vagrant (Bretherton 1989). Similarly, there are a few vagrant *Sympetrum* dragonflies which have bred in southern England, but do not do so regularly (Merritt, Moore & Eversham 1992).

Webb (1985) recognised that, in many cases, it will be impossible to decide whether a plant was introduced as a weed of neolithic cultivation, or was already established in Britain and appears in the pollen record at that time because it became more abundant in the early open fields.

Presence in previous inter-glacials is not evidence that a species is native now: *Rhododendron ponticum* reached Ireland in the Hoxnian or Gortian interglacial c 150 000 years ago (Godwin 1975), but there are no more recent fossil records, and no native occurrences of it in northern Europe since the last glaciation. Its present natural distribution is disjunct, very local in southern Spain and Portugal, and rather more widespread around the Black Sea (Tutin *et al.* 1972). Contrary to many accounts, *R. ponticum* is not a Himalayan species. Surprisingly, there seem to be some doubts as to whether the vigorous and widespread rhododendron in Britain is pure *R. ponticum* or a hybrid involving *R. catawbiense*, native in the Appalachian Mountains, eastern USA (Cross 1975). The presence of rhododendrons in Britain now is because of deliberate introduction in the 18th century.

Post-glacial fossil evidence that a species was established in Britain between the end of the last glaciation and the beginning of agriculture is almost conclusive proof of native status. The exceptions will be species which have become extinct here, and been reintroduced, such as the red squirrel (*Sciurus vulgaris*) in Scotland (Harvie-Brown 1880–81) and in Ireland (Barrington 1880), or the Scots pine (*Pinus sylvestris*) in Ireland and perhaps England (Huntley & Birks 1983; Clapham, Tutin & Moore 1987).

The very early documentation of a few species must nevertheless be treated with caution. For example, the fallow deer (*Dama dama*) is frequently described or figured in medieval manuscripts as if it were a well-known resident, yet it had been established in Britain for only a few centuries; and woad (*Isatis tinctoria*) features in Roman histories of the Celts, although it is believed to be native to southern and eastern Europe (Jessen & Halbaek 1944; Godwin 1975). In the absence of fossil evidence, a species must be shown to have arrived without human aid, which is obviously impossible to prove in most cases.

Genetic divergence: if, like caper spurge (*Euphorbia lathyris*), a species is believed to be native in some places, but an introduction in others, there might be genetic differences between populations. The native fenland swallowtail butterfly (*Papilio machaon*) differs significantly from the continental race (Hall & Emmet 1989); and there is some evidence that sticky groundsel (*Senecio viscosus*) in

natural habitats such as shingle beaches differs from populations on waste ground and railway lines (Akeroyd, Warwick & Briggs 1978). Unfortunately, very few studies of this kind have been performed, and it is a costly and time-consuming activity. It is also possible that apparent divergence can arise through founder-effects and genetic drift in a remarkably short time (eg Berry's work on house mice (*Mus musculus*) (Berry & Jakobson 1974)).

The study of enzyme polymorphisms has provided a further useful if laborious technique, which has established that some species of molluscs in the genus *Arion* are represented in Britain both by an out-crossing (long-established, probably native) and an obligately self-fertilizing (recently introduced) strain (Foltz *et al.* 1982); the same alien strains have been detected in the USA, in the absence of their sexual counterpart.

Habitat: most native species occur in 'natural' habitats, at least occasionally – sand dunes support many of the native weeds of agricultural land. Many aliens are confined to man-made sites, eg the woodlouse *Porcellionides pruinosus* in dung heaps and compost (Harding & Sutton 1985; Sutton & Harding 1989); and any species which is usually found at sites with a high proportion of certain aliens must be 'doubtful'.

Geographic distribution: an isolated population of a species hundreds of miles from the main range may be considered doubtfully native. There are exceptions, some of which can be justified as the last vestige of a once-wider range. For example, many insects associated with ancient woodland are now restricted to isolated sites (Harding 1978), or even to individual trees as in the case of *Limoniscus violaceus* (Welch 1987), some of which form a pattern. If several species show the same disjunction, it may have a natural explanation. Most species with relict distributions will occur at several scattered sites, and it may be possible to identify the features of history and management that explain their survival.

Historical evidence of introduction can be conclusive, as in the case of *Buddleia davidii*, which first appeared on sale as a garden plant in 1896 (Webb 1985). Often, however, the historical information may apply to only some of a species' populations in Britain, as perhaps in the case of caper spurge referred to earlier, which is often grown in gardens, yet has been used as an indicator of ancient woodland in eastern England (Rixon & Peterken 1975).

Rapid declines or expansions are often, though not always, symptoms of alien status. Recent colonists such as American willowherb (*Epilobium ciliatum*) obviously expand their range while becoming established. Some, such as the famous Canadian pondweed (*Elodea canadensis*), undergo an initial flush then a slower reduction in abundance. It is worth noting that aliens may represent taxonomic problems: while New Zealand willowherb (*Epilobium brunnescens*) was recognised instantly (there being no prostrate *Epilobium* in Europe), *E. ciliatum* was

confused with several natives, and overlooked, as was *Elodea nuttallii*. Some aliens, such as the corn-cockle (*Agrostemma githago*), have declined spectacularly.

Frequency of naturalisation: if a species is known to be introduced at many of its sites, the status of populations whose origin is unknown may be suspected of introduction. This applies to many liliaceous plants which are often cultivated, such as grape-hyacinth (*Muscari atlanticum*) and lily-of-the-valley (*Convallaria majalis*). At certain sites, however, they are believed to be native.

Inability to reproduce: plants which cannot set seed in Britain might be suspected to have been introduced. Thus, the ubiquitous horseradish (*Armoracia rusticana*) which rarely produces ripe fruit in Britain (Clapham *et al.* 1987) is, not surprisingly, an alien (though how it and other species become so very widespread with no obvious means of long-distance dispersal is a puzzle). Likewise, the failure of some species to breed in part of their range, such as large-leaved lime (*Tilia platyphyllos*) in Scotland (Pigott 1981), implies at least local translocation. Zoological examples are fewer, mainly because animals tend to be less long-lived than perennial plants. Migrant Lepidoptera, such as the clouded yellow butterfly (*Colias* spp.) and the silver Y moth (*Autographa gamma*), can be seen in areas well beyond their breeding range. A number of species of ant of the genus *Camponotus* have been introduced in imported timber, and survive for a short period in the vicinity of timber yards, but have not so far become established (Bolton & Collingwood 1975).

Means of introduction: if some or all of the known populations of a species are close to sources of introduced material, a strong case would be needed to prove native status. Occasionally, such circumstantial evidence can be misleading: the earliest records of the mouse-eared bat (*Myotis myotis*) were from the British Museum, Bloomsbury, prior to 1850, and from the grounds of Girton College, Cambridge, in 1888. Both are sites where one might expect to find imported animals, but equally are places where one could expect to find people capable of identifying unusual species!

All these criteria are tentative rather than absolute proof, and many indicate possible introductions rather than possible natives. They can lead one to doubt the status of a species unjustly. For instance, two beetles, *Curimopsis nigrita* and *Bembidion humerale*, were first found in Britain at a bog in South Yorkshire (Crossley & Norris 1975; Johnson 1978). For several years, they were known from no other site. Their European distribution is centred on the Baltic (ie the Yorkshire site is an extreme outlier). The site is a cut-over raised mire (arguably a man-modified habitat). At the turn of the century, a number of barges were imported from Holland (where both the species occur) for use in transporting the cut peat. There was thus considerable evidence to

Table 3. Bird species which have expanded their range and/or increased in abundance in the British Isles since 1700, and the approximate time of the increase. + indicates species which have also increased in other parts of their range. Based on information in Sharrock (1976), Cramp (1977, 1980, 1983, 1985, 1988), Fisher (1966) and Parslow (1973)

Species	Approx. dates of expansion	European expansion
Great crested grebe	1870–present	+
Fulmar	1750–present	+
Gannet	1900–present	?
Goosander	1870–present	
Oystercatcher	1900–present	
Little ringed plover	1950–present	+
Woodcock	1890–1920	
Curlew	1910–1960	+
Great skua	1890–present	
Great black-backed gull	1880–present	+
Lesser black-backed gull	1900–present	+
Herring gull	1900–present	+
Common gull	1870–present	+
Black-headed gull	1900–1980	+
Kittiwake	1900–present	+
Stock dove	1820–1950, 1965–present	+
Woodpigeon	1820–present	+
Turtle dove	1820–present	
Green woodpecker	1820–present	+
Great spotted woodpecker	1870–present	+
Golden oriole	1960–?	+
Jay	1910	?
Mistle thrush	1750–present	+
Fieldfare	1960–present	+
Black redstart	1920–present	+
Wood warbler	1850–?	?
Firecrest	1950?–present	+
Pied flycatcher	1940–?	?
Starling	1830–present	?
Siskin	1850–present	?
Serin	1960–?	+

imply possible introduction. Since then, the two species have now been found at another site which has no known Dutch connections (Skidmore, Limbert & Eversham 1987). *Curimopsis nigrita* has since been identified as a Bronze Age fossil (Buckland 1979; Buckland & Johnson 1983), which is certain proof of native status, as it is not a synanthrope.

'NATURAL' INVASIONS

In 1952, the collared dove (*Streptopelia decaocta*) was first recorded in Britain (May & Fisher 1953). In view of its 'dramatic and unprecedented spread south-west across Europe' in the previous 20 years, this individual bird was regarded by the authors as a 'pioneer of the spread rather than an escape from captivity'. Editorial comment, however, said 'Meanwhile we feel bound to conclude that no adequate evidence has so far been produced for adding

S. decaocta to the British list', but in the previous sentence remarked that 'further and less controversial occurrences will soon follow', which proved to be true. The species was first recorded breeding in 1955, and has now colonised most of Britain and Ireland (Sharrock 1976). Details of its spread across Europe are described by Hengeveld (1989).

Many other British or European birds are expanding or have recently expanded significantly. Table 3 lists some of the more dramatic examples, and indicates which have expanded over other parts of their range as well as in the British Isles. (Species whose expansion is solely due to the abatement of direct human pressures, such as birds of prey harassed by game-keepers or poisoned by pesticides, are not listed.)

One is left to ponder whether such striking changes are therefore merely a slightly more extreme example of the way most species behave in the post-glacial north temperate zone.

TRANSLOCATIONS WITHIN THE BRITISH ISLES, AND REINTRODUCTIONS

Reintroductions and translocations for the purpose of 'topping up' declining or low populations have taken place within the British Isles. In the 17th century, the red squirrel had become extremely rare or extinct over much of Scotland, due mainly to the destruction of the forests. In the 18th and 19th centuries, many reintroductions took place using stock from England (eg at Dalkeith in about 1772) and from within Scotland (eg at Minto, Roxburgh, from Dalkeith, in 1827) (Harvie-Brown 1880–81; Lever 1977). There also seems to have been a natural increase in range from the remnants of the old forest areas, into new plantations, during this period. In addition, some squirrels were released which apparently came from the Continent.

Many amateur naturalists breed native butterflies, and some release surplus adults. There has been a great increase in interest in 'wildflower meadow seed mixtures' in recent years (Wells, Bell & Frost 1981), and, although most are probably sown in gardens or in sites such as new road embankments, some have been sown in nature reserves. The motives for such activities are complex – almost always for the best of reasons, but not always with sufficient forethought for the possible consequences. The biggest problem is inadequate documentation and lack of consultation with those likely to be interested or affected (eg nature reserve managers). Are such activities really 'good conservation', or are they the naturalists' equivalent of rearranging the deck chairs on the Titanic?

The success or failure of attempts at translocation of once-native or currently rare species depends largely on careful planning and a thorough knowledge of a species' ecological needs. The reintroduction of the large blue butterfly (*Maculinea arion*) can be seen as the culmination of years of

research, originally intended to safeguard the native population, but started a few years too late. Reintroduction may be reasonable when all else has been thoroughly tried. Perhaps the public or political pressure to produce a 'positive' result in such cases makes an attempt almost inevitable.

The marsh fritillary (*Eurodryas aurinia*) is known to have disappeared from most of eastern England, largely through the drainage or improvement of old pasture (Heath, Pollard & Thomas 1984), yet a few sites exist which are now, as nature reserves, in perfect condition for this species. It is presumed that it cannot recolonise these sites naturally, so there is a choice. Some reintroductions, such as natterjack toads (*Bufo calamita*) at Sandy, Bedfordshire, are apparently outstanding successes.

One hopes that conservationists have learnt their lesson, and attempts to introduce species in areas completely devoid of suitable habitats or climate, like the release of sand lizards in the Hebrides (Lever 1977), will not be repeated: native stocks are no longer 'buoyant' enough to withstand regular 'harvesting' for translocation.

WHY ARE SPECIES INTRODUCED?

Accidents of cultivation and commerce

Sweet cicely (*Myrrhis odorata*) may be native, but has been widely grown as a culinary herb (it has a strong aniseed flavour, and was used to flavour brandy, and to mask the flavour of unsavoury meats in the days before refrigerators (Mabberley 1987)). Deadly nightshade (*Atropa belladonna*) is less easy to explain: it may have been a medicinal herb, or grown for its showy berries.

Various European amphibians have been found at or near Beam Bridge nurseries in Surrey, a horticultural nursery selling aquatic plants. Animals could have been transported as adults, larvae or as eggs amongst bundles of pond weed. Deliberate introductions of the European tree frog (*Hyla arborea*) at several sites have been unsuccessful. The reason may be that the donor populations on the Continent were almost all male: females visit ponds only briefly, to lay eggs, but males linger all summer, so are far more likely to be collected by herpetologists. It appears there is now a population established on the Isle of Wight; this species may benefit from any future climatic warming.

The brown rat (*Rattus norvegicus*) seems to have been introduced in the 18th century – 1728 or 1729 are dates widely quoted – and it probably first arrived on board ships from Russian ports (Barrett-Hamilton & Hinton 1910–21; Twigg 1975).

House mice are often transported in food, bales of straw, and other cargo. The history of island populations of this and other small rodents has been investigated in detail by Berry (1963, 1968, 1970), who has shown that significant genetic differences between island and mainland populations can

develop within a few decades. The apparent accidental transport of hedgehogs (*Erinaceus europaeus*) to off-shore islands as stowaways among plant material is discussed by Morris (1983). Hedgehogs may, on occasion, have been introduced to off-shore islands deliberately, either to control 'pests' in gardens, or for sentimental reasons. They are now perceived by many conservationists as a potential threat to ground-nesting seabirds, for which many islands are noted; as such, their translocation is to be discouraged.

There is a long list of casual records of non-British species from the vicinity of ports, such as Newcastle-upon-Tyne, but few have successfully become established. The clearest case is probably the large carabid, *Pterostichus cristatus*. This species is abundant in north-east England, and has the appearance of a native (Luff 1982): it is the commonest carabid in many riverside woods, replacing the certainly native *Pterostichus madidus* and *P. niger* locally.

Deliberate introductions

Economic motives

Rabbits (*Oryctolagus cuniculus*) were originally bred for their skins and their meat, and often proved very difficult to establish, even when they were looked after with great care! Their history has been thoroughly documented by Sheail (1971). Pheasants (*Phasianus colchicus*) may similarly have been introduced for food, probably in the 11th century; they were quite widely naturalised in the 12th century (Lever 1977).

The coypu (*Myocastor coypus*) was imported into fur farms in the 1930s, for its pelt, known as 'nutria'. Inevitably, escapes occurred, especially when the Second World War led to a lack of maintenance of perimeter fences. Up to the mid-1940s (Figure 2), there were many scattered records, but only two areas where coypu bred – in Berkshire and in the Norfolk Broads. The Broads area became the centre for a considerable population explosion, even though numbers were greatly reduced by the cold winter of 1947–48. A wetland species, the coypu burrowed into the banks of ditches and fed voraciously on reeds, and on sugar beet and other crops. In a low-lying county such as Norfolk, with much of the land close to sea level, the threat of impeded drainage was even greater than the direct losses to agriculture (Figure 3). The Ministry of Agriculture, Fisheries and Food responded with the Coypu Control Campaign in 1962. This campaign helped reduce the size of the population, and coincided with another severe winter, 1962–63; but numbers appeared to increase again in the 1970s. A further concerted trapping effort began then and continued throughout the 1980s, so that in 1989 only two were recorded (Figure 4). If the eradication of coypu has been successful, it has probably eliminated another, accidental, introduction – the host-specific parasitic louse *Pitrufulquenia coypus*.

During peaks of population size, coypu exerted a

marked effect on semi-natural vegetation. In particular, coypu numbers have been linked with the large-scale dieback of reedswamp (Boorman & Fuller 1981). Unfortunately, there is little sign of a recovery of reedswamp since the demise of the coypu. Since the 1940s, other changes, such as pollution, eutrophication and increased boating traffic, have all affected the Broads.

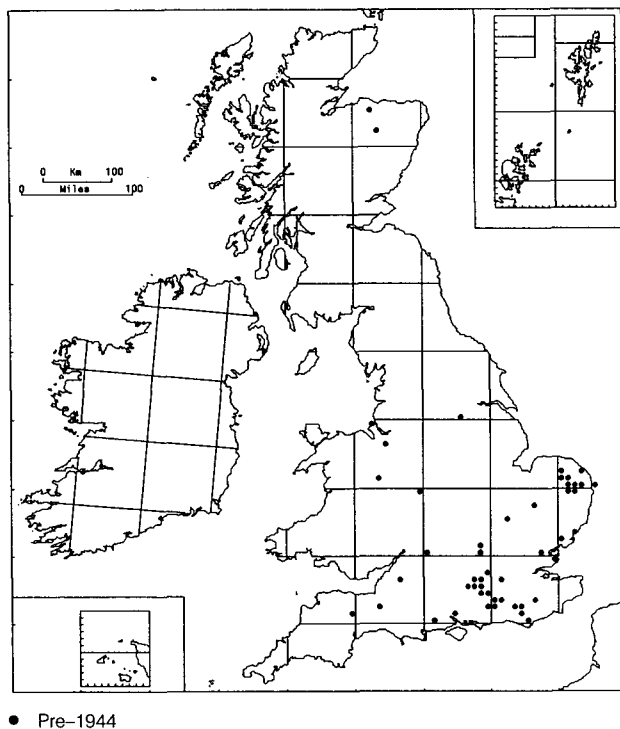


Figure 2. Records of coypu in Britain up to 1944

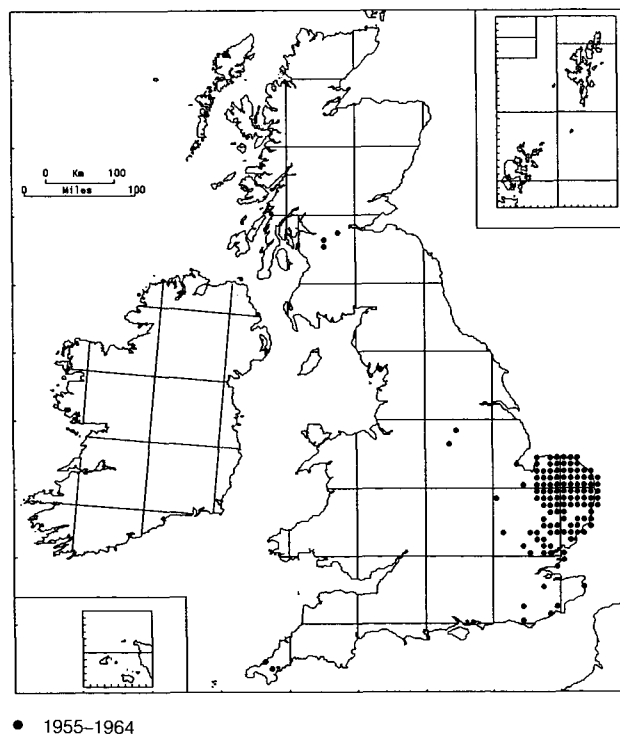


Figure 3. Records of coypu in Britain, 1955-64

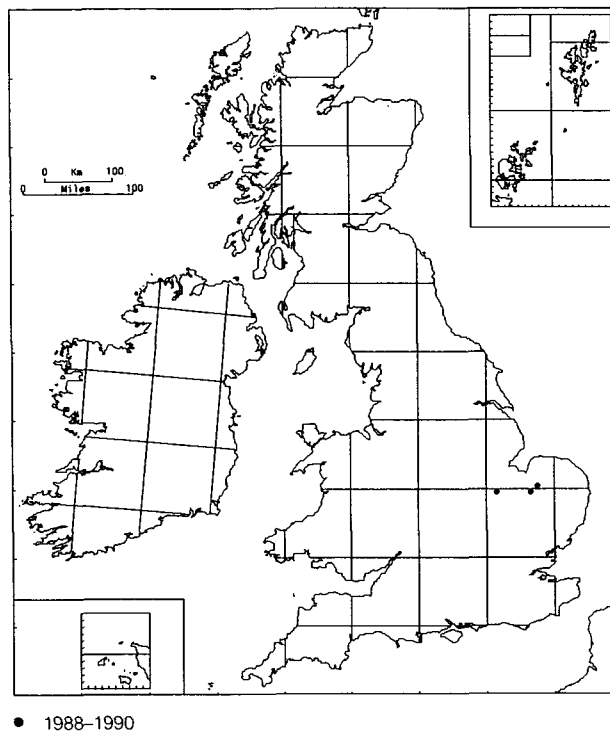


Figure 4. Records of coypu in Britain, 1988-90

Two other escapees from fur farms appear to have the potential for significant ecological impact. One, the muskrat (*Ondatra zibethicus*), has so far failed to establish itself permanently in Britain, although it has colonised parts of the adjacent Continent very successfully (Lever 1977; Gosling & Baker 1989). Feral populations in both Britain and Ireland, which established in the 1930s, were exterminated in both countries by intensive trapping programmes (Sheail 1988). The other, the mink (*Mustela vison*), is already widespread in the British Isles (Arnold 1984), and there has been speculation that it has had a severe impact, especially on waterside birds and mammals (eg Woodroffe, Lawton & Davidson 1990).

Ornamental species

The many species of ornamental waterfowl and pheasants which have been introduced into Britain are thoroughly reviewed by Lever (1977). The majority are scarcely established away from carefully managed estates. The species listed in Table 4 have maintained feral populations for many years, at least in a small area. Those marked with an asterisk may be spreading into the wider British countryside. Only the Canada goose (*Branta canadensis*), the red-legged partridge (*Alectoris rufa*), the pheasant and, in its specialised pinewood habitat, the capercaillie (*Tetrao urogallus*) have established self-maintaining populations which affect other wildlife significantly.

Another category of 'ornamental' species which have occasionally escaped or been released are cage-birds. The budgerigar (*Melopsittacus undulatus*) has bred outside the confines of free-flight aviaries at least three times on the British mainland, but seems unable to survive the more severe of

British winters. A small population on the Scilly Isles may be more permanent (Lever 1977). The ring-necked parakeet (*Psittacula krameri*) is established in two or more parts of the London area, where flocks of 20 or more are frequently seen in autumn and winter.

Table 4. Introduced wildfowl and gamebirds in Britain. Species marked * are living feral and unaided; those marked ** are well established over large areas. Data from Lever (1977), Sharrock (1976) and Hollom (1975)

** Canada goose (<i>Branta canadensis</i>)
Egyptian goose (<i>Alopochen aegyptiaca</i>)
* Mandarin duck (<i>Aix galericulata</i>)
Wood duck (<i>Aix sponsa</i>)
* Ruddy duck (<i>Oxyura jamaicensis</i>)
** Capercaillie [reintroduction] (<i>Tetrao urogallus</i>)
** Pheasant (<i>Phasianus colchicus</i>)
* Golden pheasant (<i>Chrysolophus pictus</i>)
* Lady Amherst's pheasant (<i>Chrysolophus amherstiae</i>)
* Reeves's pheasant (<i>Syrnaticus reevesi</i>)
** Red-legged partridge (<i>Alectoris rufa</i>)
Chukar (<i>Alectoris chukar</i>)
Bobwhite quail (<i>Colinus virginianus</i>)

The number of exotic plants introduced to Britain for horticulture runs into thousands, and many hundreds of species are permanently established in gardens. Of these, many occur as casuals on waste ground, roadsides and rubbish dumps, but few have invaded native plant communities. Among the exceptions are a group of three waterside plants which have successfully colonised many British rivers: giant hogweed (*Heracleum mantegazzianum*), Himalayan balsam (*Impatiens glandulifera*) and monkeyflower (*Mimulus guttatus*). One of the most successful ornamental alien plants, and certainly the one which has provoked the most active control measures from conservationists, is the rhododendron; details of its spread and habitat occupancy are given later.

Sporting

One of the few fish introductions which seems likely to have a widespread effect is that of the zander or pike-perch (*Stizostedion lucioperca*). This species has no close equivalent in Britain's impoverished native piscifuna. A sea barrier might be more effective against a freshwater fish than against almost any other organism. Unless a means of cross-Channel dispersal exists (it seems unlikely that fish eggs would stick to waterfowl feet and also be able to resist desiccation), all the species which were slow to spread in the post-glacial were unable to reach Britain.

The most carefully maintained and regularly restocked introduced fish is probably the rainbow trout (*Salmo gairdneri*). This species can affect the native fauna of a river considerably; but how much of its ecological impact (dragonflies and freshwater gastropod molluscs occur at very low densities or may be completely absent from stocked waters) is

due to artificially high population levels rather than to intrinsic features of alien species is not known.

Less conspicuously alien, but perhaps of more ecological significance, are birds of prey lost or deliberately released by falconers. The present breeding population of goshawks (*Accipiter gentilis*) in Britain is thought to result largely or entirely from this source (Sharrock 1976); Kenward (1974) suggested that 50% of all goshawks kept by members of the British Falconers' Club were lost or released. Other species of raptor are doubtless 'topped up' from formerly captive birds. Whether this number is greater or less than those illegally removed from the wild by falconers and others is unknown.

In addition to the impacts of introduced gamebirds and fish, the effect of gamekeeping on wildlife is also extremely important: forage crops sown for pheasants also support flocks of native birds and small mammals, and so attract wintering raptors such as hen harriers (*Circus cyaneus*), merlins (*Falco columbarius*) and sparrowhawk (*Accipiter nisus*) (Marshall *et al.* 1989).

Other motives

The grass carp (*Ctenopharyngodon idella*) perhaps represents a non-introduction. It is apparently unable to breed freely in Britain but it is used to manage water-weed, so it has an impact on the countryside, in just the same manner as farm livestock or as sheep used to maintain short turf on nature reserves.

The motives behind the introduction of the little owl (*Athene noctua*) were very clearly stated by those who made the introduction. For instance, Waterton, who introduced the species to his estate in Yorkshire in 1842, thought that they would be 'particularly good for the horticulturalist in his kitchen gardens'. Lt-Col E G B Meade-Waldo, who introduced little owl into Kent between 1874–80, did so in order 'to rid belfries of sparrows and bats, and fields of mice'. Eight years later, Lord Lilford, in Northants, wrote in their favour: 'they are excellent mouse-catchers, very bad neighbours to young sparrows in their nests, and therefore valuable friends to farmers and gardeners'.

By the 1930s, the little owl was well established, and had been branded a 'menace' by the Press, and was being blamed for supposed declines in songbirds such as blackbirds (*Turdus merula*) and nightingales (*Luscinia megarhynchos*), and was alleged to take gamebird chicks. The controversy became so heated, with pro- and anti-little owl factions arguing emotively, but with scant evidence, that in 1935 the British Trust for Ornithology established the Little Owl Food Inquiry. In the report of the Inquiry, the Special Committee explained that 'wide currency . . . has been given to statements that the little owl is a wholesale destroyer of game-chicks, poultry-chicks and song birds' (Collinge *et al.* 1937). The analyst, Alice Hibbert-Ware, collated a large volume of varied correspondence, and dissected many hundreds of pellets, finally concluding that 'little owls feed

almost wholly upon such insects, other invertebrates and small mammals as can readily be picked up on the ground during the hours of feeding – largely from dusk . . . to early morning' (Hibbert-Ware 1937, 1938).

The introduction of species for personal motives, or merely as a hobby, was not entirely the preserve of a small band of eccentrics. The 'Society for the Acclimatisation of Animals, Birds, Fishes, Insects and Vegetables within the United Kingdom' flourished briefly in the 1860s, but its French counterpart, 'Le Société Impériale d'Acclimatation', was apparently much more prestigious and more widely accepted: in 1861, it boasted over 2000 members, including the Emperor Napoleon III and Pope Pius IX.

LIMITS TO THE SPREAD OF ALIENS

The difficulty in evaluating the success or otherwise of particular introductions, and the possible effects on native species, are twofold. First, naturalists often ignore aliens completely, unless specifically requested for information, and this disregard is exacerbated by the exclusion of alien species from most identification guides, and the fact that no-one is quite sure of their origin. Several aliens found in Britain have proved to be new to science, and at least three are still known only from Britain: the liverwort *Telaranea murphyae* is locally abundant on the Scilly Isles; the plant bug *Neodicyphus rhododendri* probably originates in North America (Dolling 1972; McGavin 1982); the snail *Gulella io* (Kerney & Cameron 1979) is probably from tropical Africa, but is known only from hothouses in Britain and Czechoslovakia. Several species of millipede (Blower 1985) and woodlouse (Harding & Sutton 1985) also have been described from hothouses, especially at Kew, but have not been collected in the wild anywhere in the world. Should we conserve them? They could be extinct in the wild! The other difficulty in evaluating the impact of an alien is that the 'evidence' is almost always anecdotal, and based on people's initial prejudices. Considering the little owl controversy of the 1930s, one could question what solid evidence there is for the supposed effects of mink on waterfowl and small mammal populations, though there is some evidence of changes in water vole (*Arvicola terrestris*) behaviour in the presence of mink (Woodroffe *et al.* 1990). Even well-known instances, such as introduced carnivores destroying native birds in New Zealand, may be open to less sensational interpretations (King 1984).

Climatic limits

Many alien species have established in the British Isles, but have not become widespread. In a few cases, the mechanism of this range restriction is known. Hottentot fig (*Carpobrotus edulis*), for instance, is limited by temperature, especially by frosts (Figure 5) (Preston & Sell 1988); in such a case, there is clearly potential for an expansion if the British climate warms.

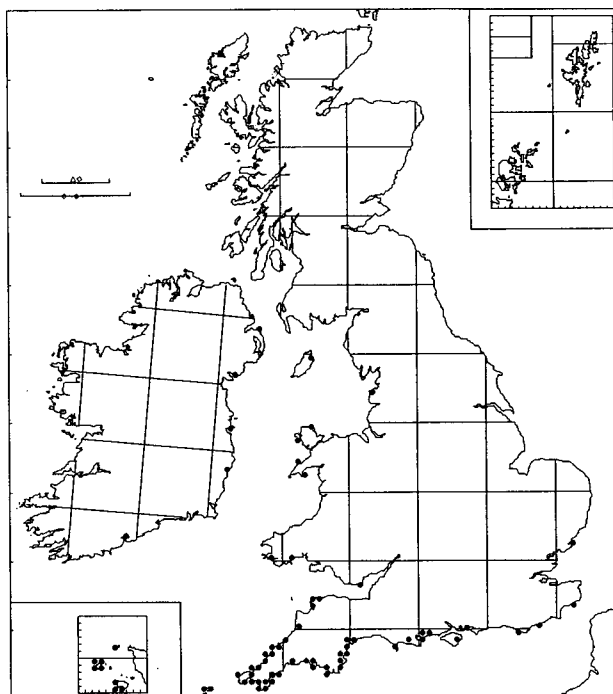


Figure 5. The distribution of *Carpobrotus edulis* in the British Isles (from Preston & Sell 1988)

Although the physiological cause has not been investigated, the Mediterranean snail (*Trochoidea elegans*) is probably likewise restricted; it is able to survive on south-facing chalk slopes, but rarely establishes elsewhere. Another snail, *Theba pisana*, has nearly all its recorded populations in or near car-parks in south-west England; this recording is not likely to be a mere reflection of conchologists' behaviour, so may imply some specific thermal characteristic of such dry, gravelly sites.

The only scorpion to become established in Britain, *Euscorpium flavicauda*, has at present a very restricted distribution, being confined to a handful of man-made sites, the best-known being Ongar railway station. Brickwork and concrete may have some resemblance to the dry, sun-baked soil or rock of the scorpion's native habitats in southern Europe. A small increase in summer temperatures could see the further spread of this remarkable exotic.

Habitat limits

On the edge of Britain's largest lowland raised mire, Thorne Moors in South Yorkshire, one of the country's first 'Garden Centres' was established in the early 1830s (Limbert 1991). By 1860, vast numbers of ericaceous shrubs were being grown: thousands of rhododendrons were raised from seed each year. A catalogue dated 1872 refers to 197 taxa of rhododendron, plus many hybrids, and 37 shrub genera. Three species survived this century: Labrador-tea (*Ledum palustre*) became extinct in about 1950; sheep-laurel (*Kalmia angustifolia*) survives and is dominant over an area of about 0.5 ha; rhododendron has become abundant over about 500 ha, nearly all of which is peripheral. Figure 6 shows this

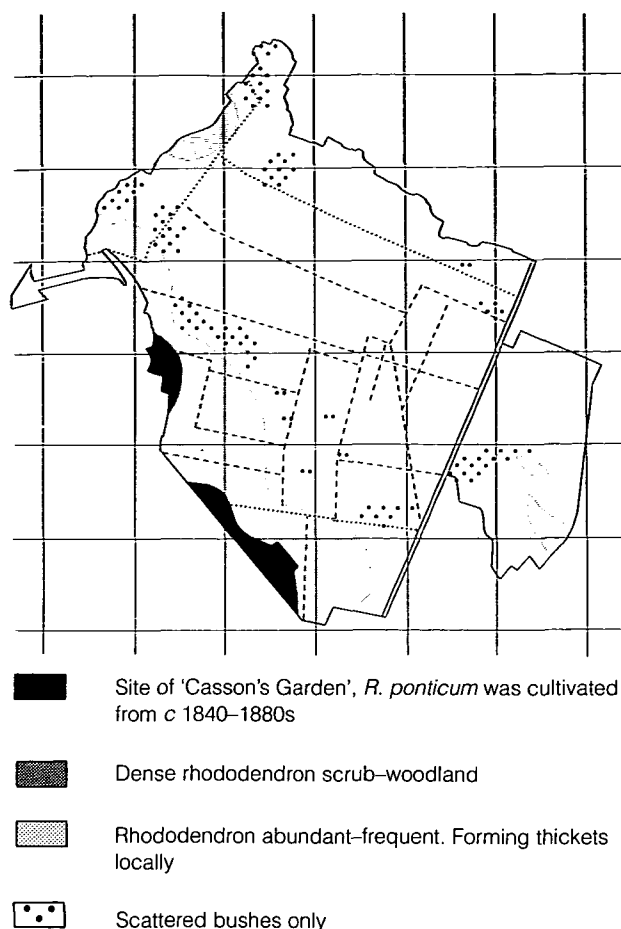


Figure 6. The spread of *Rhododendron ponticum* at Thorne Moors, South Yorkshire. Solid shading shows the location of 'Casson's Garden', a nursery where many *Rhododendron* species were cultivated c 1832–80; cross-hatching shows the area where *R. ponticum* is now the dominant shrub, to the exclusion of native species; simple hatching shows the area in which *R. ponticum* is frequent among native species; dots show isolated occurrences of single bushes of *R. ponticum* in native vegetation

area as a band along the western moor edge. The species is frequent, among native species, over about a third of the moors, with scattered individuals beyond. Rhododendron is almost absent from the central area (which was, until recent drainage, the wettest, and was covered with native vegetation). Drainage of the mire has been greatest near the edges, and perhaps the effects of fire (most severe in the drier areas) created an opening for rhododendron.

The spread of rhododendron in sand dunes, a very different habitat, has been documented by Fuller and Boorman (1977) using aerial photographs. They suggest that its establishment on the dunes was assisted by man's disturbance of the native vegetation, in this case through army activities in the 1940s creating open bare sand where seedlings could establish more easily.

Successful alien species might be expected to be generalists, able to exploit a wide range of conditions. However, some species are confined to a very narrow range of habitats. For instance, the New

Zealand willowherb occurs along the banks of streams and on wet rock faces in upland areas, and the very common ivy-leaved toadflax (*Cymbalaria muralis*) is almost confined to walls, though is occasionally found on shingle banks (Tutin *et al.* 1972; Philp 1982). It is unlikely that such aliens will compete with more than a handful of native species; and, in the case of *Cymbalaria*, there is no native species which occurs as frequently on the vertical faces of sunny walls.

Limits by dispersal

A few locally successful aliens appear to be limited by their inability to disperse. One unusual example is the tomato (*Lycopersicum esculentum*), which rarely produces seed in Britain, but is topped up from culinary sources via sewage works. Its distribution on river systems is thus almost always a downstream movement from seed sources.

The edible dormouse (*Glis glis*) is sufficiently well established in a small area of Hertfordshire to cause such domestic nuisance that Chiltern District Council has organised a trapping programme, and for the Forestry Commission to plan for its extermination as a pest (it strips bark from conifers); but, despite their fears, it seems not to have expanded its range since the 1940s (Lever 1977).

Regional variations

Even if a species is able to disperse and become established over a large part of the country, its frequency and impact may vary considerably from area to area. Three alien plants of wetlands, Himalayan balsam, giant hogweed and monkeyflower, are found beside lowland rivers and in waste places throughout much of Britain. In northern England, these species have become dominant over large stretches of industrial rivers (Figure 7; from Graham (1988)). It has been suggested that they are particularly successful where the native flora is suffering from the effects of pollution.

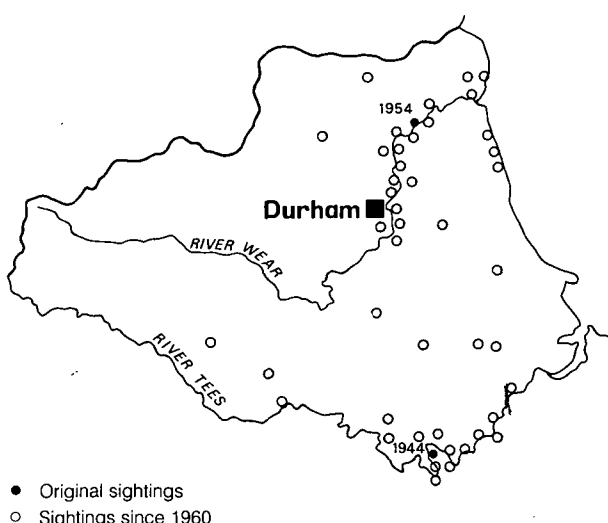


Figure 7. Spread of giant hogweed (*Heracleum mantegazzianum*) in County Durham (from Graham 1988)

One very specific form of freshwater pollution certainly assists aliens: thermal pollution. Warm-water outflows from power stations are able to support a number of species which cannot survive long term in cooler natural waters. These include the guppy or mosquito-fish (*Lebistes reticulatus*), and the submerged macrophyte *Vallisneria*. Two alien species of *Physa* (pond snails) are most abundant in artificially warmed water, but are able to survive in shallow ponds and ditches elsewhere.

The effects of warm water in rivers may occasionally extend into terrestrial habitats. Naturalised fig trees (*Ficus carica*) in the city of Sheffield are confined to the banks of the River Don, and to those parts which were formerly warmed by industrial coolant (Gilbert & Pearman 1988). All the recorded fig trees are mature, and no recent establishment has been noted. It is suggested that the trees established at a time when the Don flowed at a constant temperature of 20°C, and that, following the demise of the steel industry in the 1980s, temperatures are now too low for seedlings to establish, but mature trees are able to survive.

Ecologists' perception of the impact of an alien will be coloured by the habitat in which it is established. The rabbit, for instance, plays a vital role in maintaining open heathland on the Breck and short turf on calcareous grasslands, and these are scarce habitats valued by conservationists. Its activity in woodlands, moorlands, wetter grassland and in agricultural areas is far less sympathetically received.

Alien species, as much as natives, tend to occupy different habitats in different parts of their range. Many invertebrate species become coastal in the northern part of their range, as the low-lying coastal strip in eastern Scotland presumably has a milder climate. This fact applies as strongly to introduced molluscs, such as *Helix aspersa*, as to native ones. A wide range of molluscs which are garden species in central and south-east England are confined to glasshouses in Scotland, but are free-living in 'wild' habitats such as woodland in south-west England and in Ireland (Kerney & Cameron 1979; Eversham & Baxter 1989).

Several synanthropic invertebrates are able to survive out-of-doors in southern England. House spiders (*Tegenaria* spp.) occur in disused quarries, the house cricket (*Acheta domesticus*) may survive in refuse heaps, and the silverfish (*Lepisma saccharina*) occurs on rocks and walls, browsing on lichens and algae.

These unusual occurrences may be a simple effect of temperature, in which case global warming may cause a marked expansion of the habitats occupied by such aliens.

IMPACT OF ALIENS ON NATIVE SPECIES AND HABITATS

If a species has a very close native ally, either congeneric or with a similar ecological role, there is

more chance of direct competition, and greater potential for the native to suffer if the alien flourishes.

Theories of co-evolution should favour the native species, but the absence of biotic checks on the alien could tip the balance in the other direction: unless the alien is phylogenetically very close to the native species, it may not share its predators or, especially, parasites and parasitoids.

There are surprisingly few documented cases of direct competition between a native and an alien species. The moss *Orthodontium lineare*, a 20th century colonist from the southern hemisphere, may be ousting *O. gracile*, as they occupy a similar micro-habitat, although the alien is much more eurytopic (Smith 1977; Rose & Wallace 1974).

The most famous case of possible competition between native and alien species is perhaps that of the red and grey squirrel (*Sciurus vulgaris* and *S. carolinensis*). Kenward and Tonkin (1986) suggested that the grey is better able to digest acorns and beech mast, so is at a competitive advantage in deciduous woodland, whereas the native red is better adapted to conifers. However, if the evidence in the case of well-studied animals such as the squirrel is inconclusive, it would be correspondingly more difficult to prove competition in other, less conspicuous, species.

The question has often been asked: are some habitats much more invisable than others? And, if so, why?

Crawley (1987) tabulated the habitats of native and alien plant species, as given in the standard *Flora* (Clapham, Tutin & Warburg 1962), reproduced as Table 5. This Table shows that man-made habitats have far more aliens than semi-natural habitats. The same applies to molluscs (Table 6, derived from the modern *Field guide* (Kerney & Cameron 1979)), although there are a few differences between habitats. That these differences are not just artifacts caused by personal biases of flora and mollusc field guide writers can be shown by examining the total flora and mollusc fauna of well-recorded individual sites.

Table 5. The proportion of the vascular flora of selected habitats in Britain which are aliens. Data from Crawley (1987)

Class	Habitat	% alien
Man-made	Wasteland	78
	Walls	46
	Fields	37
	Hedgerow	22
Woodland	Conifer plantation	56
	Deciduous	5
Wetland	Bog	5
	Fen	2
Grassland	Sea cliffs	18
	Damp grassland	13
	Dunes	13
	Dry grass	5

Table 6. The proportion of alien and native land molluscs in selected habitats. Data from Kerney and Cameron (1979)

Class	Habitat	No. native	No. alien	% alien
Man-made	Glasshouses	4	15	79
	Agricultural	5	10	67
	Garden	13	18	58
	Wasteland	5	6	55
	Hedgerow	25	8	29
	Walls	10	3	23
Woodland	Deciduous	63	9	13
	Scrub	7	1	13
	Conifer plantation	7	0	0
Wetland	Marsh or fen	29	0	0
	Bog, moorland	3	0	0
Grassland	Dunes	14	7	33
	Dry grassland	15	5	25
	Damp grassland	18	3	14

Table 7. The native and alien flora of a range of sites. Data from Steele and Welch (1973), Rixon and Peterken (1975), Sage (1966), George (1961), Brookes and Burns (1970), Harding *et al.* 1988, and Payne (1978)

Site	Native	%	Alien	%
Monks Wood NNR	349	94.3	21	5.7
Bedford Purlieus SSSI	439	93.8	29	6.2
Northaw Great Wood	241	90.3	26	9.7
Dale Parish	434	88.9	54	11.1
Slapton Ley NNR	429	86.8	65	13.2
Barking Reach	162	74.3	56	25.7
Essex walls: total	203	71.0	83	29.0
on 5% of walls	31	66.0	16	34.0

Table 8. The native and alien mollusc fauna of a range of sites. Data from Steele and Welch (1973), Cameron (1978), Stratton (1964), Eversham (1991) and unpublished lists in the possession of BCE

Site	Native	%	Alien	%
Monks Wood NNR	35	94.5	4	5.4
Malham area	59	93.7	4	6.3
UEA Fen	25	92.6	2	7.4
Dale parish	30	88.2	4	11.8
Lindholme	30	85.7	5	14.3
Huntingdon (garden)	13	56.5	10	43.5

Tables 7 and 8 derive from a series of sites for which comprehensive plant and mollusc lists have been published. They show precisely the same pattern as the generalised lists. One difference is apparent: there are far fewer alien plants at some sites than others, whereas the numbers of species of molluscs is fairly similar at all but very synanthropic sites. The

proportion of aliens in the lists obviously differs depending on the size of the native fauna. For example, aliens are much more important in disturbed habitats than in ancient native woodland.

WHAT MAKES A SUCCESSFUL INVADER?

Lawton and Brown (1987) correlated body size with the proportion of successful invasions in a taxonomic group. They pointed out that the biology of large species tends to be better understood, and so people are less tempted to try the impossible. At the same time, they also emphasised population parameters (r – intrinsic rate of population increase, and K – carrying capacity) as a possible explanation of the relative success in establishing.

A more direct measure of the attention paid to a group of organisms is the amount published on the group each year. A readily available estimate is a count of the number of pages of the *Zoological Record*. If the number of pages is divided by the number of species in the group, it correlates well with the success of the group in establishing (Figure 8). So, at the higher taxonomic levels, better-known organisms are more likely to be successful when introductions are attempted, presumably because very unlikely attempts would be discounted in advance of the attempt.

Lawton and Brown (1987) noted that insects show the reverse trend – orders with mostly small species do best. An alternative explanation of this effect relies on the global distribution of the major insect orders (Figure 9). The orders with a high proportion of species living in the north temperate zone are the most successful colonists of Britain. The only large group omitted from Figure 9 are the Hymenoptera: a high proportion of described species are obligate, narrowly specific parasitoids, which cannot be expected to behave similarly to most insects. Not surprisingly, Hymenoptera lie far below the regression line of Figure 9.

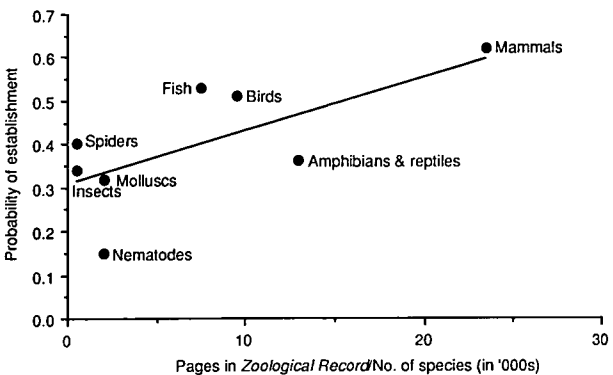


Figure 8. The relationship between the likelihood of successful establishment of alien species in Britain, and the volume of zoological literature devoted to the group (expressed as pages in *Zoological Record* in 1988, divided by the number of species in the taxonomic group)

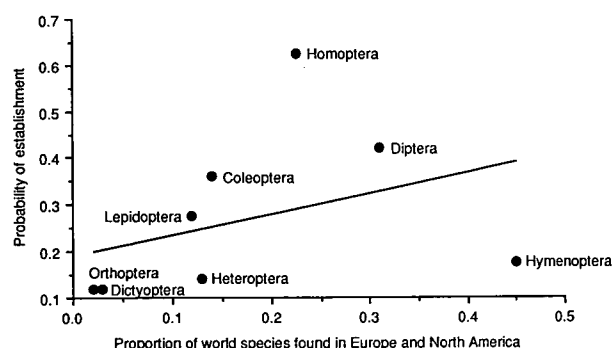


Figure 9. The relationship between the likelihood of successful establishment of alien species in Britain, and the proportion of the world fauna in the taxonomic group which is native to Europe and North America

The fact that all the estimates of world totals are gross underestimates is not a problem. As with phylum differences, a crucial factor is how well watched a group is: it is uncertain whether anyone would notice if an alien symphylian was rampaging across southern England, for instance. The most marked failures to establish are in the most thermophilous groups – amphibians, reptiles, Dictyoptera. In the latter, the documented casualties are all large tropical species; there is no recorded occurrence of an alien *Ectobius* cockroach.

Rather than seek general principles in terms of population parameters, the pattern of success and failure may be better described in terms of origins and habitats.

Crawley's list (Table 9) usefully discounted life history strategy as the key to alien success: the 'top 20' aliens include annuals (eg Canadian fleabane

(*Erigeron canadensis*)) biennials (beaked hawk's-beard (*Crepis vesicaria*)), and long- and short-lived perennials (such as American willowherb (*Epilobium ciliatum*) or sycamore (*Acer pseudoplatanus*)). Table 9 also demonstrates the diversity of dispersal mechanisms in highly successful aliens: wind-dispersed Compositae, sycamore and willowherbs, explosive pods in Himalayan balsam and rhododendron, succulent berries in snowberry (*Symphoricarpos albus*), and heavy smooth seeds in the umbellifers, whose means of dispersal are unclear. Although the list may be a little subjective, it certainly includes most of the very successful invaders of natural communities – the majority of nature reserves in Britain now seem to contain snowberry and ground elder (*Aegopodium*).

SURPRISING FAILURES AND EVENTUAL SUCCESSES

The case of the edible dormouse has already been mentioned: it is well established, and has expanded a little. It is unclear why it is not able to spread further.

The local success of porcupines (*Hystrix* sp.) in south-west England (Lever 1977; Smallshire & Davey 1989) poses the same question: if an animal is able to reach pest status in one area, why does it not become more widespread? The answer in this case, as in that of the edible dormouse, may be its lack of dispersive power in the English landscape.

These aliens are completely at home in the British climate, and are known to be able to breed successfully, and to live long adult lives. Ferrets (*Mustela furo*) can do this, and have the additional advantage of high mobility. Yet there is little factual evidence of

Table 9. The 'top 20' British alien plants (from Crawley 1987)

Species	Family	Habitat
<i>Acer pseudoplatanus</i>	Aceraceae	Woodland
<i>Aegopodium podagraria</i>	Umbelliferae	Gardens, wasteland, etc
<i>Avena fatua</i>	Graminae	Cultivated land
<i>Buddleia davidii</i>	Buddleiaceae	Wasteland, railways, walls
<i>Centranthus ruber</i>	Valerianaceae	Walls, cliffs
<i>Crepis vesicaria</i>	Compositae	Roadsides, wasteland
<i>Elodea canadensis</i>	Hydrillidae	Slow water
<i>Epilobium brunnescens</i>	Onagraceae	Streamsides
<i>E. ciliatum</i>	Onagraceae	Gardens, wasteland, etc
<i>Erigeron canadensis</i>	Compositae	Cultivated, railways, etc
<i>Impatiens glandulifera</i>	Balsaminaceae	Riversides, fens, carr
<i>Matricaria suaveolens</i>	Compositae	Tracks, etc
<i>Mimulus guttatus</i>	Scrophulariaceae	Rivers and streams
<i>Reynoutria japonica</i>	Polygonaceae	Roadsides, wasteland
<i>Rhododendron ponticum</i>	Ericaceae	Woodland, heathland
<i>Senecio squalidus</i>	Compositae	Wasteland, railways, walls
<i>Smyrnium olusatrum</i>	Umbelliferae	Roadsides and cliffs by the sea
<i>Symphoricarpos albus</i>	Caprifoliaceae	Shady wasteland, woods
<i>Veronica filiformis</i>	Scrophulariaceae	Lawns, etc
<i>V. persica</i>	Scrophulariaceae	Cultivated land

established feral populations, other than on a small number of offshore islands (Mull, Isle of Man).

The dice snake (*Natrix tessellatus*) has been predicted by several ecologists as a potential colonist, being ecologically like a grass snake (*Natrix natrix*) but rather more aquatic, and often kept by amateur herpetologists in captivity. The chances of escape thus provide a means of introduction.

The fact that the first two attempts to introduce little owls to Britain failed shows clearly that a single failure cannot be taken to indicate that a species is unsuitable or unable to compete with the resident biota. The role of chance in establishment should not be underestimated.

WHAT OF THE FUTURE?

There are more man-made habitats in Britain than ever before, providing greater scope for invasion. Likewise, the increase in disturbance to natural and semi-natural vegetation, caused by an increasingly mobile and affluent human population, and the gradual loss of indigenous species through land use change, pollution, pesticides, etc, may all make the British countryside more accessible for alien species to become established.

At the risk of jumping on an already over-crowded bandwagon, global warming will remove climatic constraints on some species, and probably increase their dispersal. Its effect on native populations and plant communities may well also increase habitat penetration by aliens.

Thus, there is a great need for more careful surveillance; BRC and the national recording schemes provide the means to carry out surveillance and to analyse the results.

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